ECOLOGY OF PLANT HUMMINGBIRD INTERACTIONS IN MASHPI, ECUADOR

Tatiana Santander, Esteban Guevara, Francisco Tobar, Holger Beck, Nicole Büttner, Andrea Nieto, Andrés Marcayata, Friederike Richter, María José Gavilanes, Cristian Poveda, Bryan Rojas, Rafael Wüest, Carolina Bello and Catherine H. Graham

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1. Introduction and project overview

One of the main hypotheses for how so many related species can co-occur is resource -partitioning where species use different resources, which limits competition among species and allows them to co-exist. In the case of hummingbirds and plants, each hummingbird species forages on a distinct set of flowers and each flowering plant species is visited by a subset of hummingbirds. Interactions between plants and hummingbirds are mutually beneficial. These mutualistic hummingbird-plant interactions are important from a hummingbird perspective because hummingbirds require nectar to fuel their high-energy lifestyles where they often hover – an energetically costly behavior – to take nectar. From a plant perspective most hummingbirds pollinate flowers as they forage on nectar, though some hummingbirds take nectar from the base of the flower, cheating the flower from this service of pollination. The intricate web of interactions between hummingbirds and their food plants evolved over millennia as a result of diffuse co-evolution which yielded a remarkable array of morphological forms and functions. On-going human activities, such as deforestation and climate change threaten these interaction webs, yet little is known as to how hummingbirds and their food plants will respond. To understand the influence of humans on this complex relationship, accurate, high quality data on hummingbird and flowering plant occurrence and hummingbird-plant interactions are required across broad regions and over an elevation range.

The Northwest slope of the Andes of Ecuador is an ideal place to study plant-hummingbird interactions because it is among the most biodiverse places on earth where multiple co-occurring species rely on each other for survival. There are ~360 species of hummingbirds on earth with the highest diversity in the Andes where up to 30 species can be found at a single site and ~1600 vascular plant species have been recorded in the region. Our study region was in the Pichincha Province (latitude 0°12′ N to 0°10′ S, longitude 78°59′ W to 78°27′ W) and covers 107 square kilometers with an elevation range from 800 to 3500 meters. Our sampling location in Mashpi reserve lies between 789 and 1315 meters along this gradient.

The goal of the project was to determine the abiotic and biotic factors driving variation in hummingbird-plant interaction networks across elevation and land-use gradients. By evaluating these mutualistic interactions we are able to predict how diversity of both hummingbirds and plants will be influenced by elevation and anthropogenic activities. The project is led by Dr. Catherine Graham from the Swiss Federal Research Institute and executed by Aves y Conservación/BirdLife in Ecuador, Santa Lucía, Maquipucuna, and Un Poco del Chocó with collaboration of several reserves including Mashpi, Las Grallarias, Amagusa, Sachatamia, Yanacocha (Fundación Jocotoco), Verdecocha, Puyucunapi (Mindo Cloud Forest), Rumisitana, Pontificia Universidad Católica del Ecuador, and Alaspungo community. In Mashpi we collaborated with Carlos Morochz, and Mateo Roldan for logistics, and Dario Medina, Anderson Medina, Kevin Cortez and Andrés Paladines were local assistants

2. Methodological Approach

To monitor abundance patterns, flowering phenology and hummingbird flower visitation we used a combination of field transects and time-lapse cameras. These transects were 1.5 km in length and were spread across the elevation and land-use gradient with 1 to 2 transects per site. We visited each of the 18 transects (11 in forest and 7 in disturbed sites) one time per month during a two year period. In Mashpi we sampled the transects from March 2017 to May 2019.

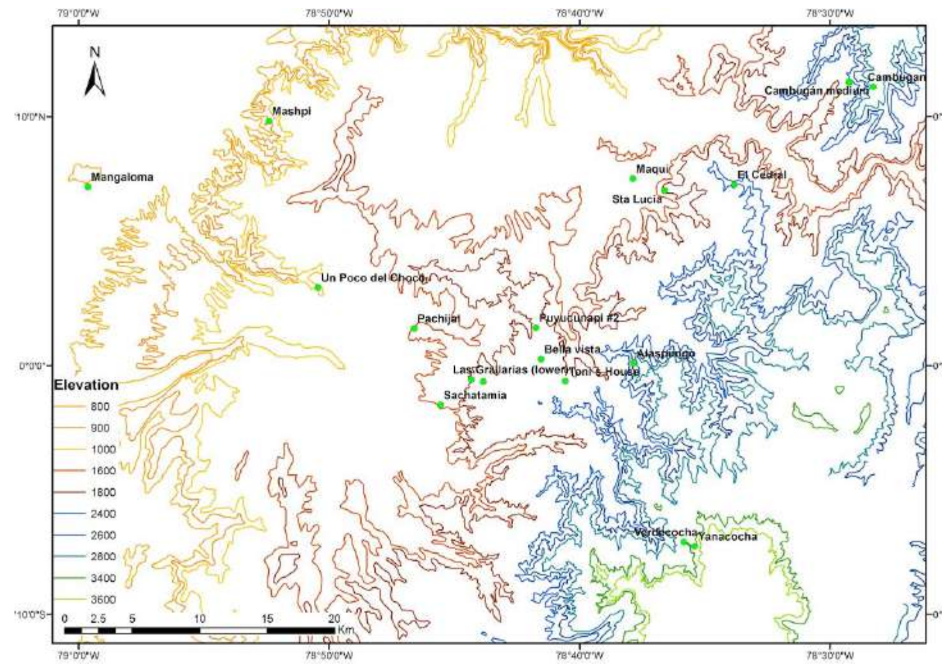

Figure 1: Location of the site in the elevation gradient.

Field transects

In Mashpi we have 2 transects of 1.5 km each. Mashpi Capuchin transect follows the Capuchin Monkey trail which it starts at 2.5 km from the entrance of the reserve and there is a sign at the main road. Once in the trail it is necessary to descend through terraces made of soft drinks plastic storage boxes. Once in the flat part of the trail our transect starts at 975 masl descending to less than 800 masl. The Capuchin Monkey trail in Mashpi Lodge is also used for butterfly trapping in the context of a different project (Figure 2).

Mashpi Laguna transect is located along the Laguna trail. The entrance of this trail is not obvious and there is not a sign but it is at about 150 m from the lodge in the main road and before the first creek that crosses the road. This transect starts at 1030 masl and ascends almost 300 m in elevation along a steep slope and it is not use for tourism purposes (Figure 3).

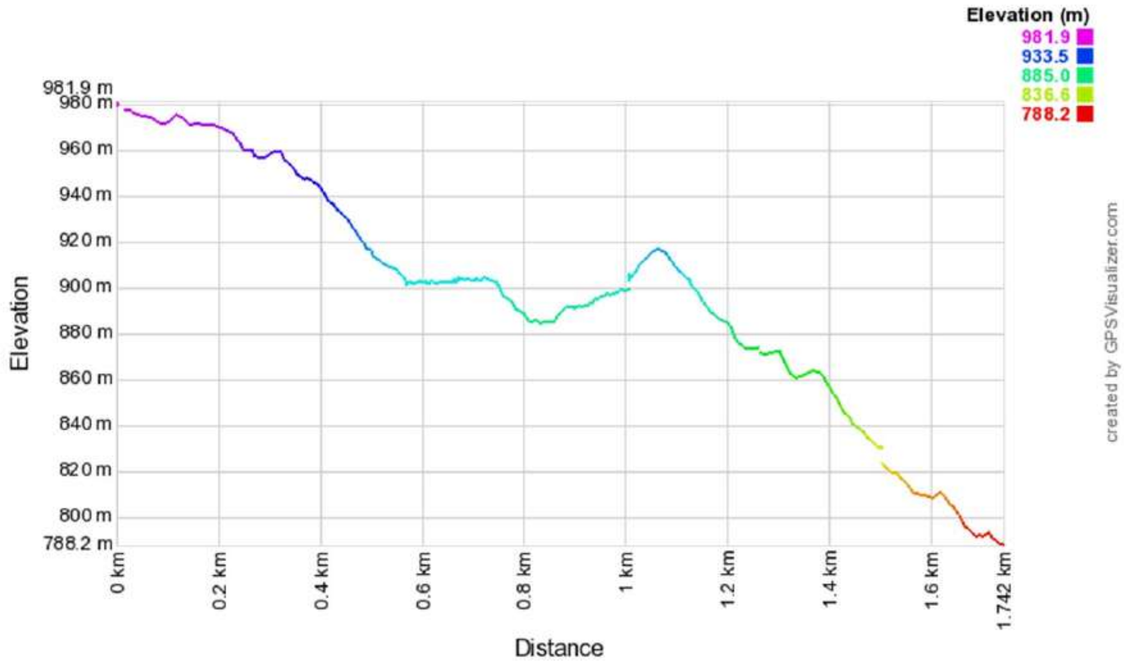

Figure 2: Elevation gradient of the transect.

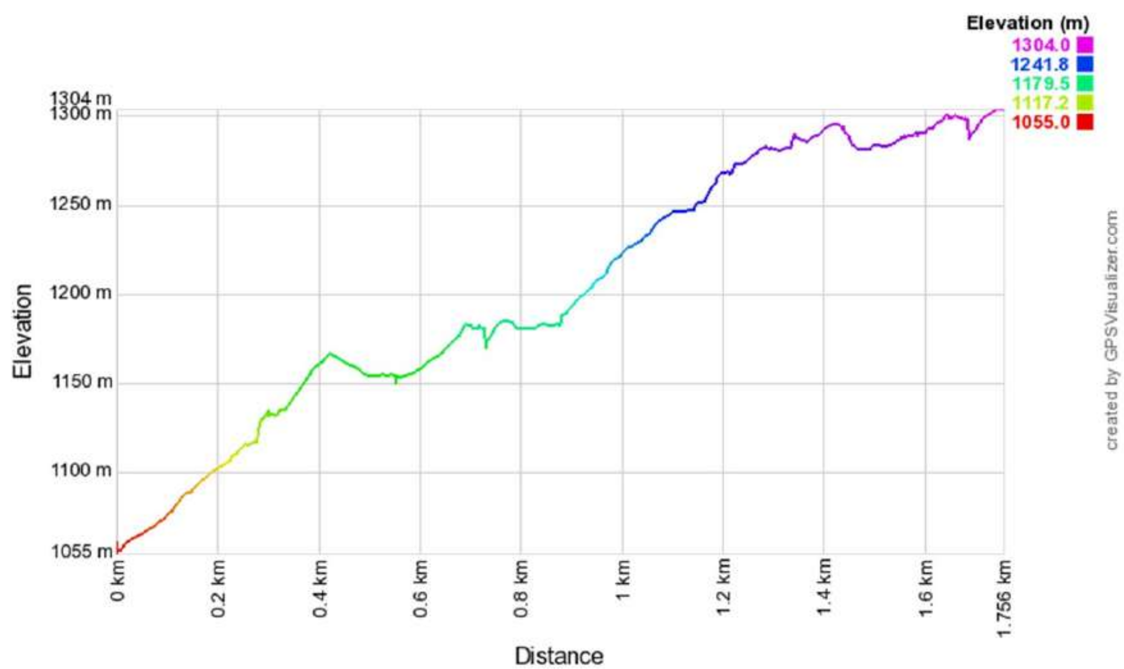

Figure 3: Elevation and location of the second transect.

Along each transect, four to five kinds of data were taken:

Figure 4: Team researcher, Andreas Nieto, counts flowers along a transect.

- **Flower counts**: Any plant with hummingbird syndrome flowers within a distance of ~5 meters of the transect was counted and identified to species. Characteristics of a flower with the hummingbird syndrome include brightly colored flowers (purple, red, orange or yellow) with medium to long corollas. While most species hummingbirds use have these characteristics we were conservative and monitored any questionable species or plants we have seen hummingbirds feeding. For each plant either all flowers were counted or in the case of bushes with more than ~100 flowers, total flowers on 5 representative branches were counted and used to extrapolate the number of flowers on the plant. Each species was collected once and pressed in order to archive our work and/or verify identification with an expert. Plant specimens were deposited at the Herbarium of Catholic University in Quito and Ibarra.

- **Interaction observations**: During the flower census, any interaction of a hummingbird with a flower was noted.

- **Hummingbird counts**: Any hummingbird heard or seen at a distance of 20 meters was also noted.

- **Flower morphology**: Several flower morphological features were measured on at least three individuals per species wherever possible. The Flower traits included were: a) flower corolla length, the distance from the flower opening to the back of corolla, b) effective corolla distance by cutting open flowers and measuring the corolla length extending back to the flower nectarines, c) corolla opening, d) stigma and anther length.

- **Nectar concentration**: This data was taken only at three sites corresponding to low, medium and high transects. Sugar concentration was collected at flowering species for up to 12 flowers per species using a refractometer (a capillary tube is used to extract nectar).

Time-lapse cameras

We used time-lapse cameras to monitor hummingbird-plant interactions. Time-lapse cameras, which take a picture every second, were placed at individual flowers along the above described transects to capture visitation by hummingbird species. We placed cameras on all flowering plants along the transect roughly proportional to their abundance. The cameras turn on at dawn and record an image every second for several days, resulting in a dataset of millions of images. These images are efficiently processed using Motion Meerkat or Deep Meerkat which can be used to sort out images with hummingbirds which can be manually identified (in the past we have been able to identify 95% of birds in images). This approach minimizes reliance on time-consuming human flower observations, greatly increasing data collection in time and space permitting a rigorous test of network theory.

Figure 5: Team researcher Holger Beck shows how a camera is set up in order to film a flower.

3. Resulting patterns

Plant-hummingbird interactions

Mashpi reserve is the place with the greatest plant diversity among our study sites, 132 species used by hummingbirds have been identified in the two transects (Annex 1). However, in our cameras we recorded 223 different interactions between 26 hummingbirds and 65 plants (Figure 6).

Figure 6: Examples of some of the hummingbirds and plants we caught in cameras.

Table 1: List of hummingbirds and number of interactions.

Hummingbird	No of interactions	No plants interacting
Phaethornis yaruqui	1014	47
Aglaiocercus coelestis	442	32
Coeligena wilsoni	337	30
Phaethornis syrmatophorus	168	19
Thalurania colombica	372	17
Phaethornis striigularis	45	13
Urosticte benjamini	114	12
Doryfera ludovicae	91	8
Ocreatus underwoodii	41	7
Schistes geoffroyi	16	7
Polyerata rosenbergi	7	5
Eutoxeres aquila	101	4
Heliodoxa jacula	22	3
Polyerata amabilis	3	3
Thalurania fannyi	10	3
Amazilia tzacatl	2	2
Androdon aequatorialis	8	2
Adelomyia melanogenys	2	1
Boissonneaua jardini	1	1
Calliphlox mitchellii	1	1
Chlorostilbon melanorhynchus	1	1
Colibri delphinae	1	1
Discosura conversii	1	1
Florisuga mellivora	1	1
Heliodoxa imperatrix	2	1
Heliodoxa rubinoides	8	1

The most common hummingbird recorded was *Phaethornis yaruqui* and the most common plant was *Drymonia teuscheri*. Both of them also interact with more species. In table 1 and 2 we can observe the number of interaction for each species.

Table 2: List of plants and number of interactions.

Plant	No of interactions	No hummingbirds interacting
Drymonia teuscheri	249	10
Psammisia caloneura	192	10
Palicourea guianensis	186	9
Schlegelia sulphurea	351	9

Aphelandra flammea	86	7
Gasteranthus lateralis	43	7
Guzmania dissitiflora	47	7
Elleanthus smithii	27	6
Glossoloma sprucei	41	6
Heliconia harlingii	194	6
Heliconia willisiana	70	6
Psammisia sodiroi	51	6
Columnea rubriacuta	142	5
Columnea sp1	61	5
Costus pulverulentus	42	5
Guzmania eduardii	58	5
Palicourea sodiroi	51	5
Pitcairnia sp4	74	5
Besleria tambensis	38	4
Calathea roseobracteata	15	4
Gasteranthus imbaburensis	30	4
Palicourea harlingii	83	4
Pitcairnia brongniartiana	79	4
Renealmia ligulata	9	4
Trichodrymonia splendens	61	4
Anthopterus wardii	21	3
Cavendishia venosa	3	3
Columnea eburnea	30	3
Columnea minor	15	3
Columnea sp2	6	3
Costus laevis	13	3
Gasteranthus corallinus	55	3
Gasteranthus pansamalanus	46	3
Glossoloma scandens	10	3
Gurania macrophylla	4	3
Psamissia pauciflora	41	3
Tropaeolum adpressum	7	3
Burmeistera belutum	6	2
Burmeistera cyclostigmata	6	2
Columnea herthae	5	2
Elleanthus arpophyllostachys	13	2
Palicourea acanthacea	2	2
Palicourea asplundii	2	2
Palicourea chimboracensis	39	2
Pitcairnia barrigae	8	2

Pitcairnia stevensonii	8	2
Psamissia ulbrichiana	35	2
Psychotria sp.	20	2
Thibaudia litensis	18	2
Anthopterus verticillatus	4	1
Besleria solanoides	7	1
Calathea ischnosiphonoides	1	1
Calathea pluriplicata	13	1
Columnea laciniata	1	1
Columnea medicinalis	6	1
Columnea parviflora	1	1
Columnea picta	33	1
Drymonia serrulata	2	1
Faramea oblongifolia	1	1
Guzmania xanthobractea	4	1
Heliconia stricta	12	1
Pitcairnia spectabilis	4	1
Psammisia pauciflora	19	1
Psittacanthus hamulifer	2	1
Thibaudia martiniana	8	1

Plants information and phenology

We recorded the abundance of flowers from March 2017 to May 2019. The months with higher abundance of flowers are November and September (Figure 7).

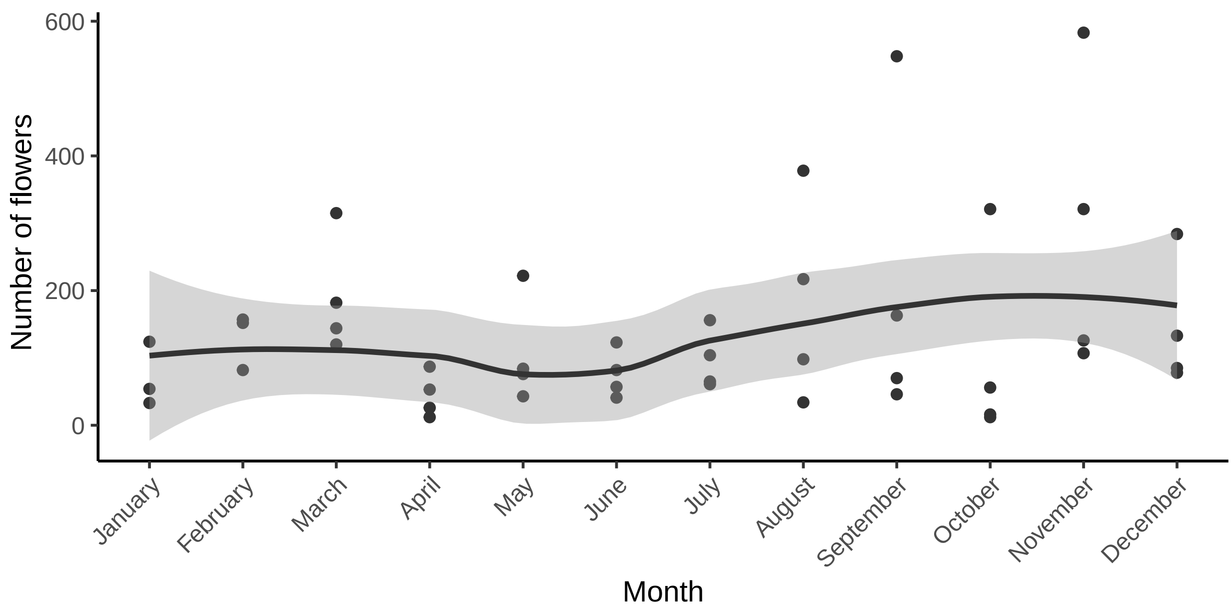

Figure 7: Abundance of flowers by month. Points represent the sum of flowers at each month and the black line represents the mean trend.

However, not all plant produces flowers at the same time. In figure 8 we can observe the phenology of the four most common plant species.

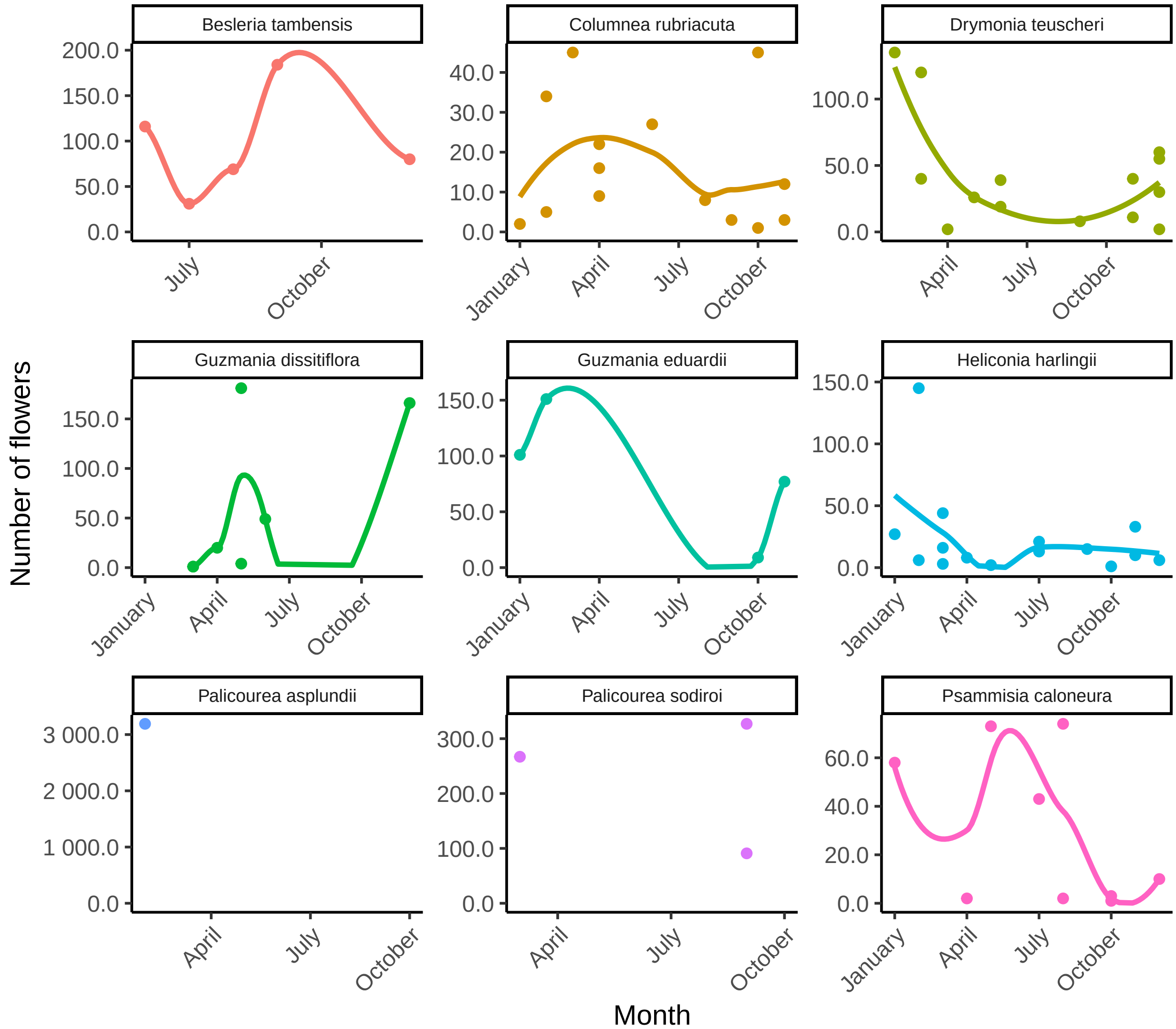

Figure 8: Phenology of most common flowers by month. Points represent the number of flowers counted in each month and the line represents the mean trend. Each color represents a different plant species.

Below we describe the most representative plant families present in Mashpi.

GESNERIACEAE

Gesneriaceae, the African violet family has around 3000 species, distributed mainly in Central and South America, East and South Asia, Europe and Oceania. In Ecuador there are 200 species grouped in 25 genera. They could be herbs (*Kohleria*, *Diastema*), shrubs (*Glossoloma*, *Columnea*) or very rarely small trees (*Shuaria*, *Besleria*). Gesneriaceae usually have opposite leaves, axillary or terminal inflorescence (cyme, raceme or fascicles), flowers with five petals joined to form a colorful tube with 4 or 5 lobes. Four didynamous stamens (two longer and two shorter) generally fused together and located at the dorsal part of the flower, a simple elongated style with the stigma usually bilobed. In the Pichincha province 15 genera and 89 species have been reported. In our study 64 species were registered, 12 are endemic, 6 are endangered (EN), and 6 are vulnerable (VU). Additionally, we found 3 species that were not previously reported for Pichincha, 2 new records for Ecuador, and 5 new species. Mashpi, with 35 species, has the greatest number of Gesneriaceae within the study area. *Columnea* (12 spp.), *Drymonia* (8 spp.), *Gasteranthus* (5 spp.), and *Glossoloma* (4 spp.) are the genus with the highest number of species. There are six endemic and threatened: *Drymonia laciniosa* is endangered (EN); *Drymonia collegarum*, *Glossoloma penduliflorum*, *Gastheranthus imbarburae*, *Gastheranthus lateralis* and *Paradrymonia splendens* are vulnerable (VU). Other important facts are *Columnea laciniate* that represents the first record for Ecuador; two new species of *Columnea* have been discovered, and *G. penduliflorum* and *Glossoloma scandens* are the first records for Pichincha.

ERICACEAE

Ericaceae also known as the blueberry family as “mortiño” is represented by 125 genera and 4000 species, widely distributed in temperate, subarctic, and also at high elevations in tropical regions. In Ecuador 21 genus and 240 species have been reported. Life forms include woody shrubs (*Cavendishia*, *Macleania*), trees (*Bejaria*, *Thibaudia*), or suffrutex (small plants with woody stems and soft branch as *Gaultheria*, *Disterigma*). Plants could be erect, prostrate or climbers with coriaceous leaves. Flowers are perfect (containing anther and stigma), mostly tubular with 4 to 7 lobes, anthers in twice number than the petals, often enlarger in one or two terminal tubes. Fruit usually is a capsule, berry or drupe. In Pichincha province there are 13 genus and 73 species. During EPHI project 45 species were registered and 18 are endemic: one is critically endangered (CR), four are endangered (EN), and 10 species are vulnerable (VU). *Macleania tropica* is the first record for Pichincha area, it was only known from Esmeraldas and Colombia. *Antoptherus ecuadorensis*, and *Macleania alata* are the first records made since the type collection in 1979 and 1986 respectively (these two species were collected nearby the study transects). Mashpi with 21 species is again the site with the greatest diversity of Ericaceae. *Psammsia* (9 spp.) by far is the genus with the highest number of species. Within this family there are six endemic and vulnerable species in Mashpi: *Anthopterus verticillatus*, *Macleania recumbens*, *Psammisia flaviflora*, *Thibaudia inflata*, *Thibaudia martiniana* and *Thibaudia litensis*.

BROMELIACEAE

Bromeliaceae belongs to the pineapple family, it is represented by 50 genera and 2000 species, restricted mainly to tropical America. Seventeen genus and 450 species have been reported in Ecuador. They are epiphytic, lithophytic or terrestrial herbs. Leaves are spirally arranged, usually rosulate (similar distribution to the rose petals), sessile (without petiole), simple, and with parallel veins. Inflorescence terminal or lateral in panicle, raceme or spike, floral bracts usually brightly colored. Flowers are bisexual or sometimes unisexual. Sepals, and petals 3, sometimes fussed forming a tube. Stamens 6 in 2 whorls of 3. The style is terminal and often 3 parted. Fruits could be berries o less often capsules. Seeds are little usually winged or plumose. In the Pichincha province 13 genera and 90 species have been reported. As part of our study 48 species were registered and 17 are endemic. One is critically endangered (CR), two are endangered (EN), and six are vulnerable (VU). In Mashpi 17 species have been registered with *Guzmania* (11 spp.), and *Pitcairnia* (5 spp.) being the most divers genus. Five species are endemic and four are threatened: *Tillandsia acostasolisii* is endangered (EN), *Guzmania pseudospectabilis*, *Guzmania alborosea* and *Pitcairnia stevensonii* are vulnerable (VU), and *Guzmania jaramilloi*. One new species of *Pitcairnia* is also present in this area.

The Network of Interactions

The interaction data we collected can be used to explore how the interactions network is organized at Mashpi. In figure 9 we show the structure of the network.

By analyzing the network structure, we found that the plant *Drymonia teuscheri* and the hummingbird *Phaethornis yaruqui* are the key species that holds the network together. If they are lost, the network will become less stable. By contrast, *Palicourea asplundii* and *Calliphlox mitchellii* are very specialized species which means they interact with a small group of specialized species.

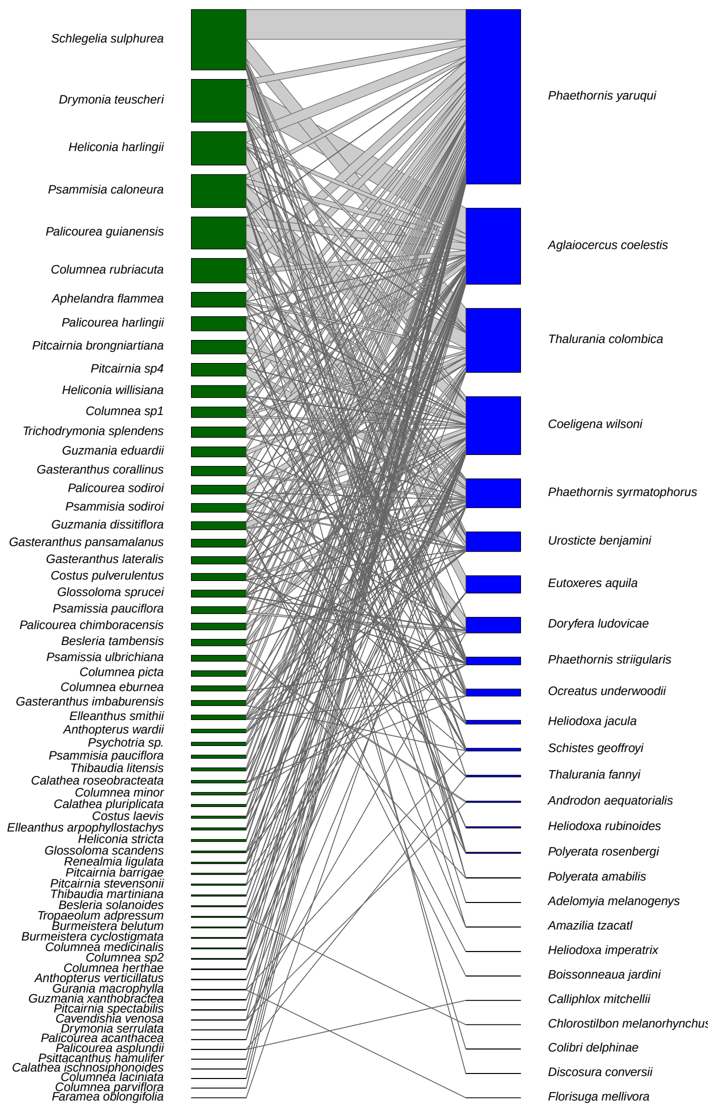

Figure 9: Network of interactions. Blue represents hummingbirds and green plants. Each line represents an interaction between a hummingbird and a plant obtained from our camera observations. Thicker lines indicate that the interaction was common while very thin lines indicate that the interaction occurred rarely. The size of the colored bar shows the number of interactions of a hummingbird or plant participated in an interaction.

4. Conclusions:

- Many similar species can occur in the same place because they use different resources.
- Conservation efforts should consider not only species but interactions among species.
- Key hummingbird plants such as *Drymonia teuscheri* and *Psammisia caloneura* can be used in restoration in Mashpi. These species offer resources to more hummingbirds than the other plants where we recorded hummingbirds foraging (14 species).
- *Calliphlox mitchellii* is the most specialized hummingbird. Species such as *Palicourea asplundii* is key to maintaining this hummingbird in Mashpi.
- Mashpi did not show a marked flowering peak. However, the months with a higher abundance of flowers are October and November.
- Mashpi is the place with the greatest plant and hummingbird diversity among our study sites.
- *Calliphlox mitchellii* and *Colibri delphinae* were hummingbird species that we only recorded in Mashpi Laguna. *Discosura conversii* , *Androdon aequatorialis*, *Polyerata rosenbergi*, and *Polyerata amabilis* were hummingbird species only recorded in Mashpi Capuchin.

Acknowledgements

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